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EVOLUTIONARY CONSEQUENCES OF EATING: *Trichosurus vulpecula* (MARSUPIALIA) AND THE GENUS *Eucalyptus*

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Abstract—While being somewhat specialized on a diet of mature *Eucalyptus* leaves (66% of feeding time), wild *Trichosurus vulpecula* consume an average of three different foods per night. Usually, these foods are two different species of *Eucalyptus* leaves, and "ground feeding." Laboratory feeding experiments indicate that this ingestion of a variety of foods is due to severe limitations on the quantity of *Eucalyptus* leaves a possum is capable of consuming. It is argued that the limitation is due to plant toxins (volatile oils, phenols) present in *Eucalyptus* leaves, rather than to "normal" nutritional factors. We hypothesize that *Eucalyptus* toxins indirectly regulate possum populations at levels that afford the *Eucalyptus* trees some degree of protection from possum predation. In addition, we suggest that the "New Zealand phenomenon" can be explained by a lack, and acquisition, of plant chemical defenses against herbivores introduced from chemically more complex environments.

Key Words—*Trichosurus vulpecula*, *Eucalyptus*, herbivore, plant chemical defenses, feeding behavior, detoxification, population regulation.

INTRODUCTION

There is a growing realization that animals do not perceive the world as green, but as a kaleidoscope of potentially deleterious chemical compounds. Freeland and Janzen (1974) attempted to demonstrate the importance of this

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difference in perception and formulated a series of hypotheses as to how a generalist herbivore can be expected to behave in order to overcome plant chemical defenses. In this paper we use an arboreal leaf-eating marsupial, *Trichosurus vulpecula*, in order to examine the hypotheses presented by Freeland and Janzen (1974). These hypotheses are (1) that a generalist herbivore has to ingest several different plant foods in order to meet its energy requirements, (2) that large amounts of a single plant food are not eaten when a generalist herbivore first encounters it, the animal initially taking small samples in preference to eating a large meal, (3) that the amount of a single plant eaten can be gradually increased as the animal gains "experience" with it, probably because the animal induces enzymes to detoxify the food, and (4) that foods lacking toxic secondary compounds are recognized quickly, larger amounts of them being eaten than can be eaten of single toxic foods, or even a restricted range of toxic foods. In addition, we hypothesize a mechanism whereby the feeding behaviors enforced by the evolution of plant chemical defenses can lead to the maintenance of predator populations at levels where the major prey item is not exterminated.

Natural History

The brush-tailed possum (*Trichosurus vulpecula*) is a solitary, nocturnal, arboreal marsupial weighing 1.5–2.5 kg (Dunnet, 1956). It is found over much of the forested areas of Australia, its natural habitat being grassy and shrubby *Eucalyptus* forests (Troughton, 1951). Populations reach densities of 2.2 possums per hectare and exhibit little or no fluctuations in size within a given year or from one year to the next (Winter, personal observation). There are usually two breeding seasons per year although a female will often not breed during the second, minor breeding season (Dunnet, 1964; Smith *et al.*, 1969). A single young is produced. When the young is about 9 months of age the mother drives it away (Winter, personal observation). Most young do not manage to establish a home range. This age class is subject to considerable mortality (Dunnet, 1964). If a young animal does establish a home range, it may remain there for up to 6 or more years (MacLean, 1967). *T. vulpecula* is a leaf eater (Gilmore 1967; Mason 1958), and in Australia the majority of its diet is mature *Eucalyptus* foliage.

Mature *Eucalyptus* leaves contain large concentrations of volatile oils and phenols (Baker and Smith, 1920; Penfold and Willis, 1961). *T. vulpecula* lacks the type of complex stomach (Tyndale-Biscoe, 1973) that would be expected to maintain a bacterial flora capable of degrading plant secondary compounds prior to their reaching the absorptive surfaces of the small intestine. Brush-tailed possums must rely on other means to protect themselves from the toxic effects of *Eucalyptus* secondary compounds. Hinks (1956) and

Hinks and Bolliger (1957*a,b*) found that *T. vulpecula* fed *Eucalyptus* leaves produced large concentrations of glucuronides in the urine. When fed non-toxic, artificial diets (domesticated vegetables) possums produced only small amounts of glucuronides in the urine. Animal microsomal enzymes degrade toxic plant secondary compounds via a two-phase reaction (Williams, 1959). The second of these phases involves the conjugation of the modified toxin with glucose or some other molecule such as an amino acid or sulfate group. These glucuronides are excreted in the urine. From this it would appear that microsomal enzymes of *T. vulpecula* protect it from the potentially toxic effects of its food.

Habitat

The study area was near Brisbane, Queensland (latitude; 27°33′ S; longitude, 152°56′ E), in a slightly disturbed open forest. The forest originally had a shrubby understory. Selective tree felling and the grazing of cattle have converted it into an open grassy forest. Most of the trees in the forest are in the genus *Eucalyptus* (*E. tesselaris, E. territicornis, E. crebra, E. hemiphloia,* and *E. maculatus*). Other common species include *Angophora subvelutina* and *Tristania suaveoleus* (Myrtaceae), *Acacia alocarpa* (Leguminosae), and several species of rain-forest tree (including *Ficus* sp.) along a nearby river. The species and location of all trees were mapped with a plane table and each tree was individually marked.

METHODS AND MATERIALS

Feeding Behavior in the Wild

During a study of *T. vulpecula* social organization (Winter, in preparation), observations on 1 of 6 possums (3 males and 3 females) were made 1 night a week for the 12 months December, 1965, to December, 1966. During any one night a single possum was followed with the aid of a spotlight and binoculars. The possums had been individually marked, and the location of each individual's den tree was known. A night's observation began by waiting for the possum to emerge from its den. The possum was followed all night until it retired in the early morning. During observation the location of a possum (on the ground, in a particular tree, etc.) and what its behavior was (feeding on a particular species of plant, traveling, grooming, resting, etc.) were recorded at least every 5–6 min. Records were taken more frequently when behavioral changes occurred. For the purpose of analysis an hour was divided into tenths. Any behavior recorded in a particular tenth was taken to have been in progress for the whole of that tenth.

Individual possums differed in their response to the light. Extremely shy possums could be followed only at a distance of 50–60 m, and the light frequently had to be dimmed with orange cellophane paper, a diaphragm, or the light was not shone directly on the possum. Most individuals rapidly became accustomed to the light and could be followed at distances much shorter than 50–60 m. Nights when a possum retreated to its den in response to the light, spent long periods of time (e.g., 1 hr) staring back at the light, or was mislaid for more than an hour, were eliminated from the sample. This left a total of 36 nights of observation: 7 nights with Gus, 5 with Alec, 5 with Jack, 6 with Gert, 6 with Jill, and 7 with Alice.

Cage Feeding Experiments

Feeding experiments were designed to determine: (1) how the amount of *Eucalyptus* leaves eaten differed between when an individual was fed a single species of *Eucalyptus*, and when it was provided with three *Eucalyptus* species; and (2) how much artificial food (low toxic plant secondary compound content) would be consumed by possums after having been fed nothing but *Eucalyptus* for varying periods of time, and how this compared to the amount of *Eucalyptus* that would be consumed after similar periods of time feeding on nothing but *Eucalyptus*.

The species of *Eucalyptus* leaves chosen for the experiments were those known to be "preferred" by free-living *T. vulpecula*. Where possible, leaves were removed from individual trees known to be fed on by possums. To ensure that all individuals would eat while in captivity, possums were kept on an artificial diet for 5 days prior to beginning the experiments.

Experiment 1. Two possums were fed *E. crebra* leaves (and nothing else) for a period of 5 days. Leaves were replaced daily and the net weight of the leaves placed in the cages was recorded. When the remaining leaves were removed 24 hr later, they were oven-dried at 60–70°C. In no case did a possum eat all the leaves provided. Control bunches of leaves were oven-dried each day. This provided a conversion factor for determining the dry weight of leaves eaten by individual possums per 24 hr. After 5 days on the *E. crebra* diet, the possums were given access to three species of *Eucalyptus*: *E. crebra*, *E. territicornis*, and *E. hemiphloia*. Determinations of the dry weight consumption per day were made for each leaf species. This was continued for 5 days. Two similar experiments were carried out, differing only in the species of *Eucalyptus* fed to possums during the first 5 days. Two possums received *E. hemiphloia* and two others received *E. territicornis*.

Experiment 2. Individual possums were fed *Eucalyptus* leaves for varying periods of time, and then placed for 5 days on an artificial unnatural diet of white bread, pumpkin, and apples. These foods are not usually regarded as containing large concentrations of toxic plant secondary compounds. One possum was kept on *Eucalyptus* leaves for 8 days, one for 5 days, two for 4 days, and three for 2 days. Records were taken of the amounts of unnatural foods consumed.

RESULTS

Field Observations

Observations throughout the study revealed that possums eat a wide variety of food types (Table 1). About half of these different food types were consumed on only one or two occasions. The bulk of the diet was made up of mature *Eucalyptus* leaves supplemented with seasonally available foods such as flowers and fruit of the mistletoe *Amyema miquelii*. This predominance of *Eucalyptus* in the diet is reflected in the results of the 36 nights of following individual possums. Feeding on mature *Eucalyptus* leaves made up 66% of the total observed feeding time. Of this, more than three quarters is accounted for by feeding on *E. territicornis* and *E. hemiphloia* (Table 2).

The next most important type of feeding behavior is ground feeding. This took place on 35 of the 36 nights and accounted for 23% of the total feeding time. Ground feeding involves the consumption of a variety of foods, few of which could be accurately identified. Not all possums had access to cattle-feeding troughs. Because of this inequality, and as feeding from troughs accounted for only 3% of the total feeding time, it is included as ground feeding.

Of the remaining 11% of the feeding time, 5% was spent feeding on the leaves, flowers, etc., of four non-*Eucalyptus* tree species, and 6% was spent eating flowers and fruit of mistletoe (Table 2).

Over the 36 nights of observation an average of three different foods were consumed per night. Two types of food were eaten on 7 nights, three foods on 18 nights, four foods on 7 nights, and five foods on 4 nights. As ground food was consumed on 35 of the 36 nights, this estimate of number of foods per night is conservative since ground food is many different things.

At least one species of *Eucalyptus* was eaten each night. If three foods were eaten, the food additional to one *Eucalyptus* and ground food was usually a second species of *Eucalyptus*. Only once were all three foods *Eucalyptus*. If four foods were taken, they were ground food, two species of *Eucalyptus*, and either an additional species of *Eucalyptus* or one of the non-*Eucalyptus* foods listed in Table 2. If five foods were eaten, the fifth food was usually non-*Eucalyptus*. When two foods were eaten, one was *Eucalyptus*, and the other ground food.

We have been forced to use the amount of time spent feeding on particular foods as an estimate of feeding. An amount of time spent eating leaves is

TABLE 1. TYPES OF FOODS OBSERVED TO BE EATEN BY *Trichosurus vulpecula* DURING THE COURSE OF FIELD WORK

Food items	Frequency of eating[a]
Eucalyptus territicornis	
(mature leaves, buds, young capsules)	Frequent, nonseasonal
E. hemiphloia	
(mature leaves, blossoms, buds, young capsules)	Frequent, nonseasonal
E. crebra	
Mature leaves	Frequent, nonseasonal
Young leaves	Rare
E. tesselaris (leaves)	Occasional
E. maculata (leaves)	Occasional
Amyema miquelii (a mistletoe) (flowers, buds)	Frequent, seasonal
Euroschinus falcatus (berries)	Seasonal
Angophora subvelutina (mainly young leaves, blossoms)	Frequent, seasonal
Tristania suaveoleus (leaves)	Occasional
Ficus sp. (leaves)	Rare
Ipomea cairica (a vine) (leaves)	Two observations
Mallotus philippinensis (leaves or fruit)	One observation
Acacia alocacarpa (leaves)	Occasional
Lantana sp. (flowers)	One observation
Hawk moth larva	One observation
Cicada exuvium	One observation
Insect gall on branch of *E. maculata*	One observation
Agaric fungus (ground)	One observation
Low vegetation (ground)	
Grasses (assorted species)	Probably
Coranopus didymus (leaves)	Probably
Solanum nigrum (leaves)	Probably
Aphananthe philippinensis	Probably
Passiflora suberosa	May have killed male 6228
Available through man's activities (ground)	
Cattle feed (lucerne and millet mixture)	Frequent
Bean sprouts	One observation
Sprouting grain in cow pat	One observation
Dried peas	One observation

[a] Ingestion of each food type is indicated in a qualitative way.

TABLE 2. AMOUNT OF TIME SPENT FEEDING ON PARTICULAR FOODS DURING 36 NIGHTS OF OBSERVATION OF INDIVIDUAL POSSUMS

Food item	No. of nights eaten (36 max.)	Average time per night	Total time spent eating	Percent of total feeding
Eucalyptus territicornis	31	1.28	39.6	66%
E. hemiphloia	12	1.54	18.5	
E. crebra	16	0.58	9.2	
E. tesselaris	3	0.57	1.7	
E. maculata	1	0.50	0.5	
Angophora subvelutina	4	0.58	2.3	5%
Tristania suaveoleus	3	0.63	1.9	
Ficus sp.	2	0.30	0.6	
Euroschinus falcatus	1	0.90	0.9	
Amyema miquelii	8	0.81	6.5	6%
Ground feeding	35	0.70	24.5	23%

not comparable to a similar amount of time spent on ground feeding. For a possum, feeding on *Eucalyptus* leaves is simply a matter of ingesting leaves. There is little or no search time involved. Ground feeding involves a larger search component. Possums feeding on the ground continually moved from place to place, ingesting small amounts of food at a time. For example, possums were observed to feed on grass. However, they selected young growth rather than dry, rank grass. Tender young grass was scarce during most of the

TABLE 3. PROPORTION OF FOOD EATEN OVER 10-DAY EXPERIMENTAL PERIOD THAT WAS EATEN DURING THE FIRST AND SECOND SET OF FIVE DAYS

		Percentage of total food eaten over the full 10 days	
Food for first 5 days	Possum	First 5 days (one *Eucalyptus* sp.)	Second 5 days (three *Eucalyptus* spp.)
Eucalyptus crebra	1	31.65	68.35
	2	28.65	71.35
E. territicornis	3	31.53	68.46
	4	7.48	92.52
E. hemiphloia	5	25.98	74.01
	6	38.31	61.70

year, and possums had to search for it. In terms of quantity of food ingested per unit time, leaf feeding was far more profitable.

Feeding Experiments

Experiment 1. The amount of food ingested when possums were fed one species of *Eucalyptus* for 5 days was consistently smaller than the amount ingested when the same possums were provided with three species of *Eucalyptus* for 5 days (Table 3). During the first 5 days the amount ingested per day

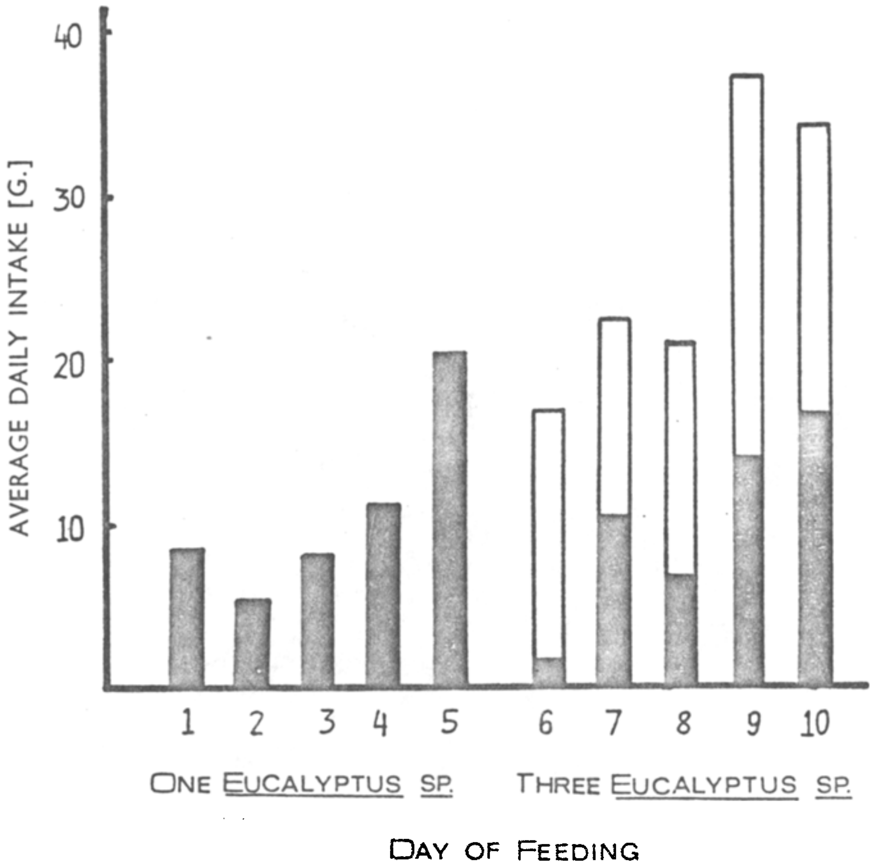

FIG. 1. Average dry weight of leaves eaten per day of the experiment. Consumption of the species provided during the first 5 days of the experiment is indicated by black shading; consumption of the two additional species (provided during the second 5 days) is indicated by the unshaded area.

increased such that the average amount consumed on the fifth day was approximately twice the average consumed on the first day (Figure 1). When possums were given three species of *Eucalyptus*, there was a similar pattern of ingestion. The average amount consumed on day 10 was approximately twice that eaten on day 6 (Figure 1).

Increasing ingestion during the second 5 days was not due to continued increases in consumption of the *Eucalyptus* species eaten during the first 5 days. Rather, it was associated with a form of sampling behavior. Small quantities of two species were eaten on the sixth night, and there was a sampling of a different combination of two species on the seventh night. Not until the last two nights of the experiment did most individuals eat all three species over a 24-hr period. Possums ate more food when feeding on all three species of *Eucalyptus* than they did on any other night. The increase in ingestion during the second 5 days was due to an increase in the number of species eaten in a day, and a gradual increase in the amount of each species eaten.

The average of the maximum amounts each possum ate in any one day when provided with one *Eucalyptus* species is approximately half that of a similar average from when possums were fed three species (Table 4). These average maximum dry weight consumptions per day were converted into kilocalories using a value of 5.4 kcal/g dry weight of leaves. This value is taken from Marples' (1973) data on the caloric content of food in the stomachs of *Schoinobates volans* (the stomachs contained nothing other than *Eucalyptus* leaves, flower buds, and a little bark). Assuming a 60% digestive extraction of the food's energy content, a diet of one *Eucalyptus* species does not provide enough energy to maintain the standard metabolic rate of a 2.19-kg possum (the average weight of the possums used in the experiments). A diet of three *Eucalyptus* species provides for the standard metabolic weight

TABLE 4. ESTIMATION OF CALORIC VALUES OF THE AMOUNT OF FOOD INGESTED AND ASSIMILATED BY 2.19 KG POSSUM FED DIETS OF ONE AND THREE SPECIES OF *Eucalyptus*

	Average maximum dry weight eaten in 1 day	Caloric value (5.4 kcal/g)	Caloric value of assimilated food (60%)	Energy to maintain SMR for 1 day
Possums fed one *Eucalyptus* sp.	21.96 g	118.6 kcal	71.16 kcal	122.29 kcal
Possums fed three *Eucalyptus* spp.	43.63 g	235.6 kcal	141.37 kcal	

(Table 4). A 60% digestive assimilation is simply a rather generous estimation of what could be expected for a nonruminating mammal of this size (Golley, 1967). Standard metabolic rate is taken from Dawson and Hulbert's (1970) data on *T. vulpecula*. If the daily energy requirement is increased by 20% to allow for specific dynamic action, movement, etc. (increased to 146.75 kcal/day), a diet of three *Eucalyptus* species may be just sufficient. A 20% increase in energy requirement is probably too small, the 60% energy assimilation far too generous, and to this must be added the cost of metabolizing the leaf toxins and providing glucose molecules to form glucuronides with the metabolized toxins. If a possum can balance its energy budget on a diet of nothing other than three species of *Eucalyptus*, it is only just doing so.

Experiment 2. When possums were fed nothing other than one species of *Eucalyptus* for periods of 2, 4, and 5 days, and then switched to a diet of apples, white bread, and pumpkin (less toxic artificial diet) for 5 days, the average consumption was 1 apple, 2½ slices of bread, and 170 g wet weight of pumpkin per day. This is equivalent to 74.3 g dry weight of food per day. A similar rate of consumption of artificial food was recorded for a possum following a diet of one *Eucalyptus* for 5 days, and then three species of *Eucalyptus* for 3 days (8 days on a *Eucalyptus* diet).

Consumption of 74.8 g dry weight of nontoxic food per day is much greater than the average maximum consumption of possums given three species of *Eucalyptus* (Table 4). The total caloric content of the daily nontoxic food intake was 302.27 kcal. Caloric values for the artificial foods are taken from Altman and Dittmer (1968). A 60% digestive assimilation would provide a possum with 181.36 kcal/day when feeding on the artificial foods. This is greater than the energy assimilated from three species of *Eucalyptus* leaves (Table 4). It is also greater than the 146.37 kcal hypothesized as the daily energy requirement.

DISCUSSION

During the first 5 days of the feeding experiments individual possums did not ingest enough *Eucalyptus* leaves to meet normal body maintenance requirements. When provided with three *Eucalyptus* species, the possums may have ingested enough to meet these requirements. This limitation in the amount of food eaten was not observed when possums were given artificial foods. These observations can be interpreted as being the result of two mutually exclusive physiological phenomena. *Eucalyptus* leaves of all three species could be nutritionally lacking or imbalanced in some way, so limiting the quantity of leaves ingested. On the other hand, the quantity of leaves ingested could be limited by the rate at which possums are capable of detoxifying *Eucalyptus* secondary compounds. The less restricted consumption of artificial foods could be the result of these foods being less nutritionally lacking, or their being less toxic.

Nutritional factors do not seem to be related to the limited ingestion of *Eucalyptus* leaves. Species of *Eucalyptus* leaves differ little in their gross nutritional content, having 3–7% fat, 6–9% protein, 37–42% carbohydrate, and 6–9% fiber (Pratt, 1937). If nutritional imbalance is the basis of the observed limitation, it must be the result of the leaves lacking minor nutrients. For more leaves to be eaten when three species are provided than when a single species is given, the lack of some minor nutrient in each species must be complemented by the presence of minor nutrients in the other species. While such a phenomenon need not be impossible to imagine, it does not account for the increase in ingestion over the first 5 days of the experiments. When mammals are fed nutritionally lacking or imbalanced diets they will initially eat the food, but soon exhibit feeding depression or a complete refusal to eat the food provided (Rozin, 1967). Feeding depression is also observed in animals fed foods containing digestive inhibitors (Glick and Joslyn, 1970). The observed increase is the reverse of this process: rather than a growing dislike, it is an increase in appreciation for the food. This, together with there being little difference between the gross nutritional content of *Eucalyptus* leaves and that of the artificial food, militates against nutritional factors being the basis of the limited *Eucalyptus* ingestion. In the proportions eaten, the artificial foods had an overall content of 0.9% fat, 2.2% protein, 17.03% carbohydrate, and 0.85% fiber (Altman and Dittmer, 1968). If anything, *Eucalyptus* leaves are the slightly better food.

The presence of plant secondary compounds can explain the possums' limited ingestion of *Eucalyptus* leaves. *Eucalyptus* oils and phenols are known to be toxic to mammals (MacPherson, 1925; Read et al., 1970). As mentioned earlier, possums fed *Eucalyptus* leaves produce much greater quantities of urinary glucuronides than do possums fed less toxic domesticated vegetables (Hinks, 1956; Hinks and Bolliger 1957*a,b*). Glucuronides are the metabolic products of microsomal detoxification. It appears that possums absorb and have to detoxify *Eucalyptus* secondary compounds.

Detoxifying mechanisms have to be induced (Conney and Burns, 1972; Freeland and Janzen, 1974). The occurrence of a toxic effect from a foreign compound is dependent on the rate of detoxification, and the quantity of compound ingested. Toxic effects can be eliminated if the compound is ingested at a rate such that the detoxifying enzymes are not overloaded. The quantity of a toxic food that an animal can safely ingest can be expected to increase as enzymes are induced for detoxification. Obviously there is some limit to the quantity of a food that can be safely ingested and detoxified. This process can explain the increase in ingestion of a single *Eucalyptus* species during the first 5 days of the experiment. It can also explain the limited ingestion of this species during both 5-day periods.

The increase in ingestion during the second 5 days can be explained by induction of additional enzymes to process different toxins present in the two new *Eucalyptus* species. This second phase of increasing ingestion was characterized by two phenomena. First, there was sampling behavior leading to the ingestion of all three species by the ninth and tenth days. Second, on day 6 there was a drastic reduction in ingestion of the *Eucalyptus* species eaten during the first 5 days. Possums either abandoned the species they had been eating and sampled the two new species, or continued to eat some of the old while sampling one of the new. When feeding on a food that is not supplying minimum energy requirements it is obviously advantageous to eat, or attempt to eat, additional foods when they are available. However, when foods are added to an already toxic diet, there is potential for additive, synergistic, or inhibitory interactions to occur among the toxins (Freeland and Janzen, 1974). The potential danger of an additive or synergistic interaction can be minimized by treating both new and old foods in the same way: in combination they can be equally dangerous. Once the potential for detrimental interaction has been assessed by sampling behavior, consumption of large amounts of the old food (for which enzymes have already been induced) and some of the new food can take place. This pattern was observed during the second half of the experiment (Figure 1). The active sampling and later consumption of all three species, the continued limited ingestion of single species, and the continued restriction in total energy intake make it unlikely that continued increase in ingestion could have taken place had only a single species been provided during the second 5 days.

This explanation assumes that different *Eucalyptus* species contain different types of oils and phenols. Although each of the three species used contains oils that are present in one or the other species, the combination of oils in each is different, and two of the species contain at least one type of oil not found in either of the other two species. The quantitative composition of the oil content also differs between the species (Penfold and Willis, 1961; Baker and Smith, 1920). Nothing is known of the phenolic composition of the three species. The observed patterns of *Eucalyptus* ingestion are compatible with an interpretation based on the toxic secondary compound content of *Eucalyptus* leaves. This interpretation also explains the ingestion of large quantities of artificial (low toxicity) foods associated with an apparent absence of a period of enzyme induction.

Consequences of the Experimental Results

Marsupials and *Eucalyptus* can be assumed to have been evolving together since Australia abandoned Gondwanaland some 45–56 million years ago (Raven and Axelrod, 1972; Tyndale-Biscoe, 1973). Leaf-eating marsupials, in this case *Trichosurus vulpecula*, can be expected to have had an impact on the evolution of *Eucalyptus* antipredator characteristics. *Eucalyptus* chemical defenses are effective in limiting the quantity of *Eucalyptus* leaves individual *T. vulpecula* can eat over a given time period. Individual possums can, however, eat enough *Eucalyptus* to account for the majority of their energy requirements. In the wild, 66% of their feeding time is feeding on species of *Eucalyptus*. For *Eucalyptus* chemical defenses to be effective against possums, they must in some way be directly or indirectly responsible for limiting the number of possums feeding on individual trees. In other words, the chemical defenses must in some way limit the size of the possum population.

The inability of possums to gain all their energy requirements from a single species of *Eucalyptus* is evidenced by free-living possums feeding on an average of three different foods in any one night. Possums fed on *Eucalyptus* every night, but they also went in search of non-*Eucalyptus* foods 35 out of 36 nights. This resulted in 34% of the feeding time being spent eating difficult-to-get foods. They are difficult to get for the following reasons. Most of the 34% was taken up eating a variety of foods found on the ground and involved a large search effort. These ground foods are widely scattered through an animal's home range, and occur in small parcels. In terms of quantity of food ingested per unit time, feeding on *Eucalyptus* leaves was far more profitable than ground feeding. The remaining non-*Eucalyptus* foods can be characterized as being either seasonal in occurrence (e.g., mistletoe flowers and fruits) or as being in some way "unpalatable" (probably due to toxic secondary compounds) as evidenced by the very small amount of time spent feeding on them (e.g., *Ficus* sp. leaves, see Table 2). These non-*Eucalyptus* foods are necessary for a possum to be able to balance its energy budget, and these foods are either temporary, in short supply, or somewhat inedible. This necessity to consume other foods is probably reflected in the carelessness of male 6228. He was observed to have paralyzed hind limbs as he left a *Passiflora suberosa* vine (an introduced plant). He was never seen again. *Passiflora* is extremely toxic, and paralysis is a classic symptom of *Passiflora* poisoning.

We hypothesize that the density of *T. vulpecula* populations is indirectly limited by the occurrence of toxic secondary compounds in its major food item. Although the possums can eat enough *Eucalyptus* to make up the majority of their energy requirement, they have to consume non-*Eucalyptus* food in order to subsist. These other foods are in short supply, and it is this that limits the size of the possum population, rather than the abundance of the major food item.

Also, in this indirect way, *Eucalyptus* species have obtained protection from the depredations of possums. In the next section we examine evidence that supports the proposal.

The New Zealand Phenomenon

The flora of New Zealand evolved in the absence of mammals, or of any ecological equivalent to an arboreal leaf-eating mammal. From 1840 to the early 1920s *Trichosurus vulpecula* were introduced to New Zealand in order to foster a previously nonexistent fur trade (Pracy, 1962). When introduced to particular forests, the possum population rose rapidly, frequently reaching levels of 29–49 individuals per hectare (Kean and Pracy, 1953; Batcheler *et al.*, 1967). This rapid increase in population density was not due to any change in litter size, number of breeding seasons, age of sexual maturity, or longevity. There appeared to be an increase in juvenile survivorship (Tyndale-Biscoe, 1955, 1960, 1973). In Australia the only potentially important possum predators are domestic dogs. These are also present in New Zealand. Predator release does not seem to be the basis of the New Zealand possum population explosion.

Associated with these rapid increases in possum density was destruction of many individuals of particular tree species. These species were highly "palatable" to possums (Kean and Pracy, 1953; Zotov, 1949). Following this denudation of the forests, the possum populations declined to approximately 14 individuals per hectare (Batcheler et al., 1967). Tree species that in many cases had been almost eliminated gradually recovered as new individuals grew (Kean and Pracy, 1953; Gilmore, 1967). These new individuals were less "palatable" to possums than individuals of the species had been, and certain other tree species increased in importance as possum food (Kean and Pracy, 1953; Gilmore, 1967). Trees were no longer killed by possums, and the possum population did not exhibit any further rapid population increase (Kean and Pracy, 1953).

The rapid increase in density of newly introduced populations can be explained as being due to the presence of an abundance of relatively nontoxic foods. These did not require an individual possum to search for additional foods in order to make up its energy budget. Individuals could, and did, concentrate their feeding activities to one or two trees, ultimately killing them (Kean and Pracy, 1953). Selection due to possum feeding eliminated "palatable" trees, and selected for trees of low "palatability." Loss of "palatability" is associated with the presence of plant defenses, usually toxic secondary compounds (Freeland and Janzen, 1974). The feeding patterns of New Zealand possums can now be expected to be similar to those of Australian possums. Indeed, possums living in areas of New Zealand that have had possums for a long time consume an average of three different types of foods a night (Gilmore, 1967). The situation closely resembles that in Australia. Trees have evolved defenses against possums, possum populations are stable, and although the quantity of potential food need not have changed, food trees are no longer denuded.

The proposed mechanism for evolutionary regulation of predator carrying capacity depends on prey chemical defenses forcing predators to search for and consume other foods. By forcing one of its predators to feed on foods other than it, the prey is automatically providing the selective force necessary to help bring about resistance to the predator in these other prey populations. Assuming that the predator's ability to overcome prey defenses does not change, increased resistance to predation among these additional prey times must lead to an even greater decrease in the size of the predator population. A limit to the resistance of prey populations to predation is imposed by some level of cost–benefit to individual prey (e.g., Janzen, 1973). This can be expected to depend on the plant part that the predator eats, the plant life form, successional stage, etc. (Janzen, 1969; Cates and Orians, 1975). In turn these limits will ultimately stabilize the predator density at some particular level. The apparent inability of *T. vulpecula* to specialize on a *Eucalyptus*-only diet is probably an evolutionary compromise related to the costs and benefits of locating and consuming non-*Eucalyptus* foods, as opposed to energetic and time costs, involved in processing a more toxic all-*Eucalyptus* diet.

SUMMARY

Field observations and laboratory experiments on the feeding behavior of brush-tailed possums (*Trichosurus vulpecula*) support hypotheses on the feeding behavior of generalist herbivores (Freeland and Janzen, 1974). These were:

1. A generalist herbivore has to ingest several different plant foods in order to meet its energy requirements.
2. Large amounts of a single plant food are not eaten when a generalist herbivore first encounters it, the animal initially taking small samples in preference to eating a large meal.
3. The amount of a single plant eaten can be gradually increased as the animal gains "experience" with it, this probably is a result of the animal inducing enzymes to detoxify the food.
4. Nontoxic foods are recognized quickly, larger amounts of them being eaten than can be eaten of single toxic foods, or even a restricted range of foods.

We hypothesize that *T. vulpecula* populations are indirectly regulated by chemical defenses evolved by their major plant food: *Eucalyptus* spp. The evolution of these defenses is at least in part due to selection induced via possum feeding. Actual limitation of the possum population, and so protection for the *Eucalyptus* trees, is achieved via the chemical defenses forcing individual possums to consume food other than *Eucalyptus*. It is the availability of these other foods that limits the density of *T. vulpecula* populations. The hypothesis is compatible with the New Zealand phenomenon. On being introduced to New Zealand, possum populations reached extremely high densities, followed by severe reduction in density and the occurrence of stable populations. This was associated with possum-induced selection for less palatable (probably more toxic) food tree species. Populations of other generalist herbivores can be expected to be limited by self-induced evolutionary changes in the chemical defenses of their food plants.

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